THE OLDEST FRESHWATER DECAPOD CRUSTACEAN, FROM THE TRIASSIC OF ARIZONA

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ABSTRACT. The oldest known freshwater crayfish is described here from a nearly complete specimen found in the Chinle Formation of Late Triassic (Late Carnian) age in Petrified Forest National Park, Arizona, USA. It differs significantly from other Triassic crayfish and is placed in *Enoploclytia porteri* sp. nov. in the family Erymidae (Malacostraca, Decapoda). Except for clam shrimps (Eubranchiopoda) and notostracans *E. porteri* sp. nov. is the only crustacean that has been described from the non-marine Upper Triassic strata of North America.

THE fossil record of crayfish (Malacostraca, Decapoda) is rather sparse and consists primarily of isolated appendage fragments (Schram 1986). Definite early Mesozoic non-marine forms were unknown until the nearly complete specimen described here was collected from the Chinle Formation of Late Trassic Age in Petrified Forest National Park, Arizona, USA (text-fig. 1A, B). Although the fossil (text-figs. 2A, B and 3) is similar to fossil shrimp of the family Penaeidae, it is distinguishable as a crayfish and is assigned to the genus *Enoploclytia*, in the family Erymidae. The specimen differs in significant features (e.g. long, slender first pleopods, lack of carapace and chelae ornamentation—see reconstruction in text-fig. 4) from other species of *Enoploclytia* and is placed in the new species *porteri*.

Crustacea are generally scarce in the non-marine Upper Triassic strata of North America. The most abundant are clam shrimps (Eubranchiopoda) which have been described from the Chinle Formation in New Mexico (Tasch 1978) and the Newark supergroup of eastern North America (Bock 1953; Olsen *in* Bain and Harvey 1977; Olsen *et al.* 1978). Notostracans have also been described recently from the Newark Supergroup of eastern North America (Gore 1986). Olsen (*in* Bain and Harvey 1977) has reported the occurrence of a supposed crayfish in the Newark Supergroup in North Carolina. However, that fossil has never been described and the drawings published by Olsen are not clear enough to evaluate satisfactorily.

The fossil described here has been deposited in the natural history collections at Petrified Forest National Park (PEFO), Arizona.

GEOLOGICAL SETTING

The Chinle Formation is widely distributed in the Colorado Plateau area of the south-western United States where it ranges up to about 400 m in thickness. It is composed principally of structureless variegated mudstone and many relatively thin, discontinuous beds of grey and tan sandstone and conglomerate together with minor amounts of non-marine limestone (Stewart *et al.* 1972). The formation was deposited in a broad basin by streams and in lakes during the Carnian and Norian Stages of the Late Triassic (Ash *et al.* 1986). Although about a dozen lithologically distinctive members have been recognized in the formation only the Petrified Forest and Owl Rock Members are exposed in the Petrified Forest (Billingsley 1985). The Chinle is estimated to be about 350 m thick in the vicinity of the Petrified Forest (Stewart *et al.* 1972).

Many types of fossils occur in the Chinle Formation including enormous quantities of petrified wood and large numbers of leaves, cones, and palynomorphs (Ash 1974*b*; Litwin 1985). Invertebrate fossils, including gastropods and bivalves, horseshoe crab trackways, insect remains, and clam shrimps are also found in the formation (Breed 1972). Vertebrate remains are locally abundant and consist of the remains of many types of fish, several species of amphibians, and many taxa of reptiles

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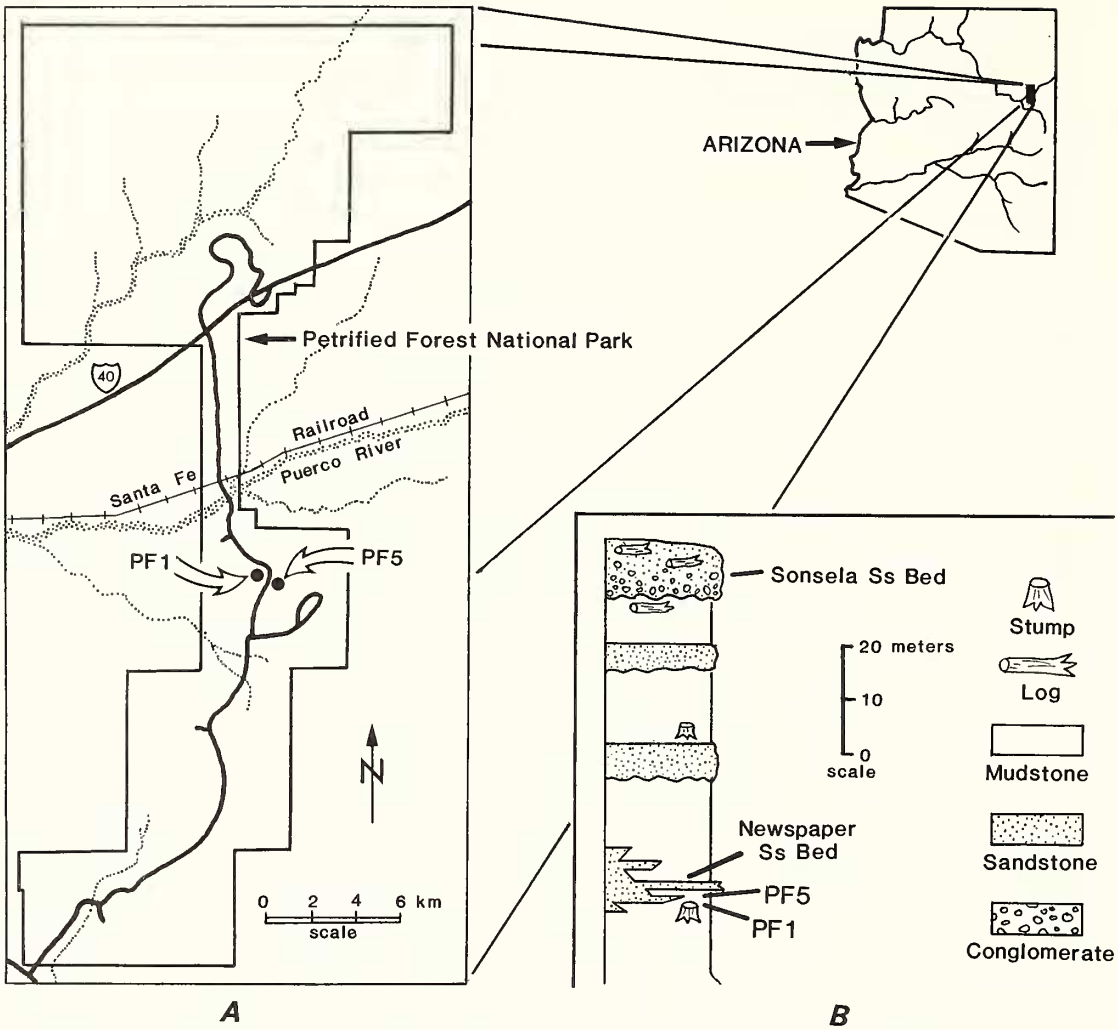


TEXT-FIG. 1. A, map of Petrified Forest National Park, Arizona showing the location of the fossil localities and geographic features mentioned in the text. B, composite stratigraphic section of the lower part of the Petrified Forest Member of the Chinle Formation in the vicinity of fossil localities PF1 and PF5.

including dinosaurs (R. A. Long, pers. comm., 1985). Recent investigations show that the largest known concentration of all types of fossils known from the Chinle Formation are found in Petrified Forest National Park.

Locality

The crayfish described here was collected from a locality about 5·5 km south-east of the Puerco River in Petrified Forest National Park, Arizona (text-fig. 1A). The locality (PF5 of this report) is situated in some low hills about 120 m east of the main park road in the SW1/4, NW1/4, sec. 23, T. 18 N., R. 24 E. and is the same as the University of California Museum of Paleontology (UCMP) fossil plant locality P3901-4 (Daugherty 1941). It is about 100 m east and 2 m stratigraphically higher than the principal fossil leaf locality (locality PF1 of this report and UCMP fossil plant locality P3901-1) but in the same

bed of structureless grey mudstone (text-fig. 1B). Locality PF5 is about 55 m below the Sonsela Sandstone Bed in the lower part of the Petrified Forest Member. Several thin beds of the Newspaper Sandstone Bed are present on the slope just to the west of the crayfish locality and another is about one metre above the locality. Locality PF5 is in the *Dinophyton* floral zone of Ash (1980) which correlates with the Late Carnian Stage of the Upper Trassic (Ash *et al.* 1986).

Many fossils of several types occur scattered throughout the bed of grey mudstone at locality PF5, including the carapaces of an unidentified clam shrimp, beetle elytra, a number of plant megafossils, and the crayfish. Daugherty (1941) reported the occurrence of three fossil plants at the locality: *Dadoxylon chaneyi*, *Equisitites* sp., and *Lycostrobus chinleana*. Additional plant fossils have been collected from the locality by the second author including *Neocalamites* sp. and *Zamites powellii*. Three deeply weathered stumps of trees that resemble *Araucarioxylon arizonicum* are exposed a few metres to the east of the locality in the same bed of grey mudstone.

MATERIAL

The description is based on a single, fairly complete, laterally compressed specimen which is preserved as part and counterpart that are more or less separated along the mid-sagittal plane into right and left halves (text-figs. 2A, B and 3). As shown in the figures, most of the left and right first pereiopods and right pereiopods two to four are preserved. The telson is fragmentary however, and the uropods are absent. The fossil does not appear to have been altered appreciably since burial. Fine details are visible as a consequence of the fine-grained nature of the rock in which it is embedded. The fossil is described and reconstructed here as an astacid crayfish (text-fig. 4).

SYSTEMATIC PALAEONTOLOGY

Class MALACOSTRACA
Order DECAPODA
Infraorder ASTACIDEA Latreille, 1803
Family ERYMIDAE Van Straelen, 1924
Subfamily ERYMINAE Van Straelen, 1924
Genus ENOPLOCLYTIA McCoy, 1849
Enoploclytia porteri sp. nov.

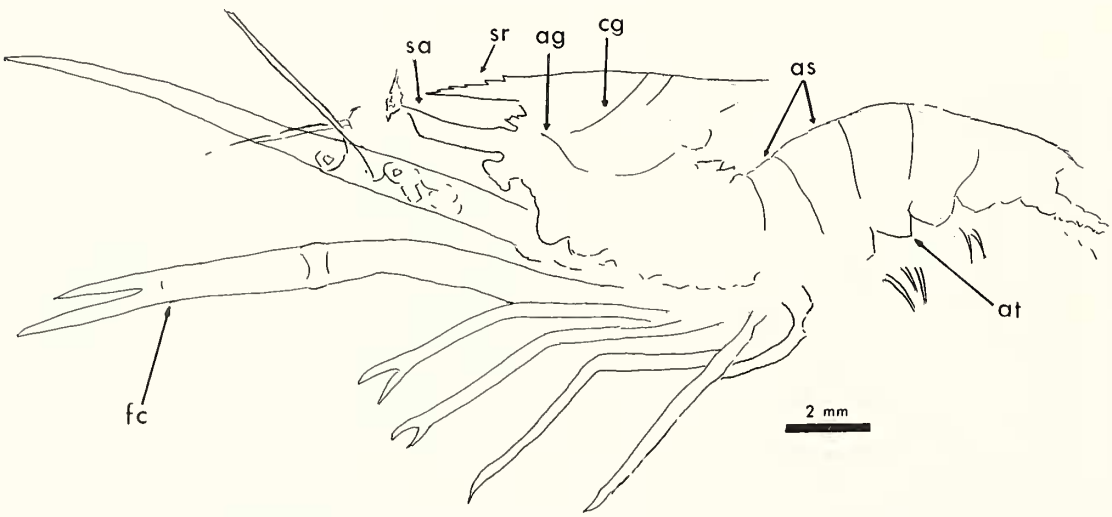
Text-figs. 2A, B and 3

Type specimen. Holotype PEFO 2991. Late Carnian, lower part of the Petrified Forest Member of the Chinle Formation in Petrified Forest National Park, Arizona.

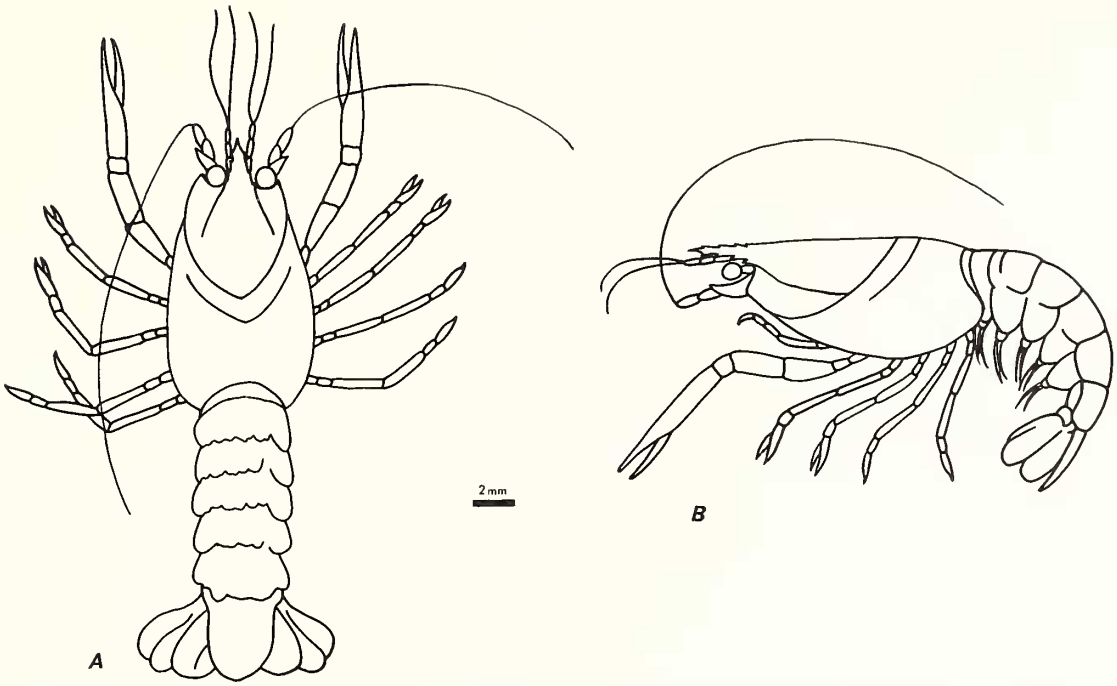
Derivation of name. The trivial name honours Mr David Porter who discovered the only known specimen of the species.

Diagnosis. Specimen small (length 2·5 cm, from most posterior part of telson to anterior tip of rostrum; total length 3·8 cm, from most posterior part of telson to anterior tip of first pereiopod). First pereiopod long (protopod length 1·8 mm, endopod length 15·7 mm), slender with narrow chelae (left 5·4 mm, right 5·6 mm). Chelae width does not exceed that of distal portion of leg. Pereiopods two and three with small chelae (average length 1·2 mm), chelae toothless. Chelae of pereiopod two slightly larger than chelae of pereiopod three. Pereiopods four and five lacking chelae. Pereiopods two to five are about the same length, 9·8–10·5 mm (10·6, 9·8, 10·1, 10·5 mm total length legs two to five respectively). Cephalothorax subcylindrical. Carapace length 11·1 mm (tip of rostrum to most posterior part), depth 5·3 mm at deepest. Carapace unornamented, rostrum spiny, well developed (length 3·0 mm). Cervical, postcervical, and antennar grooves present. Abdomen length 10·7 mm. Pleopods slender, equal in length. Abdominal segments with well-developed pleura. First abdominal segment approximately half the width of the second and somewhat shorter.

TEXT-FIG. 2. *Enoploclytia porteri* sp. nov. from the Upper Triassic of Petrified Forest National Park, Arizona, USA. A, right half, × 3. B, left half, × 3.



TEXT-FIG. 3. Outline drawing of the right half of the fossil showing the slender first chelae (fc), segment of antenna (sa), spiny rostrum (sr), antennar groove (ag), cervical groove (cg), first and second abdominal segments (as), and lobed abdominal tergites (at).



TEXT-FIG. 4. Reconstruction of *Enoploclytia porteri* sp. nov. Note that the first pleopods are slender and the second and third chelae are about the same size. A, dorsal view. B, lateral view.

Affinities. The astacid crayfish share some important characteristics with fossil shrimp of the family Penaeidae such as well-developed pleura, a spiny rostrum, and long slender chelae. However, the new specimen differs significantly from penaeids in several important respects. In astacids, as in the fossil described here (text-fig. 4), the first pereiopods are chelate whereas in most penaeids the second or third pereiopods bear the chelae. In penaeid groups where the first pereiopod is chelate, it is small (e.g. *Antrimpos*, see Glaessner 1969) or there are other significant diagnostic characteristics present (e.g. the distinctive rostrum of *Bylgia*, see Glaessner 1969). Moreover, with respect to other characteristics of the pereiopods, the most distinguishable group of penaeids (*Aeger*, Schram 1986; Glaessner 1969), and also some members of less cohesive penaeid groups (e.g. *Antrimpos*, see Glaessner 1969) bear distinct spines on the largest (and other) pereiopods. No such spines are visible in the fossil described here (text-figs. 2A, B and 3). Furthermore, the first and second abdominal segments of penaeid shrimp are generally equal in width and height (Glaessner 1969). In the new fossil, the first segment is distinctly narrower and shorter than the second segment; the typical astacid condition. Thus, it is concluded that the fossil most probably represents an astacid crayfish.

The placement of *Enoploclytia porteri* sp. nov. within the family Erymidae is based primarily on the presence of cervical and postcervical grooves, and the subcylindrical carapace (cf. text-figs. 2A and 3). Within the Erymidae, the Eryminae is distinguished from the Clytiopsinae (in which Förster 1967 places only *Clytiopsis* and *Paraclytiopsis*) by the presence of an intercalated plate and large chelae on the first pereiopods. Also the Eryminae generally have better developed rostra, and may exhibit ornamentation on the carapace and pereiopods. Although the presence of an intercalated plate cannot be observed in this fossil it is placed in the Eryminae because of the longer first chelae, and the presence of a well-developed rostrum. *E. porteri* sp. nov. is excluded from the erymid genus *Eryma* because of the shorter rostrum and stouter first chelae of that genus.

DISCUSSION

The early history of the decapod crustaceans is poorly known. The earliest may be *Palaeopalaemon newberryi* (Schram *et al.* 1978) from the Upper Devonian of North America, although Felgenhauer and Abele (1983) have an alternate view of the systematic affinities of that fossil (see also Brooks 1969). The earliest post-Devonian decapods known from North America are the marine species *Pseudoglyphea mulleri* (Van Straelen 1936) from the Upper Triassic of Nevada and the undescribed, fragmentary fossil which has been attributed to a crayfish from the Upper Triassic Newark Supergroup in North Carolina (Olson in Bain and Harvey 1977). Thus *Enoploclytia porteri* sp. nov. is the oldest described freshwater decapod, predating *Enoploclytia* from the ?Middle Jurassic of Europe, *Erymastacus* from the Lower Jurassic of Canada, and *Eryma* from the Lower Jurassic of Europe (Glaessner 1969).

Zoogeographically the new species is of interest because of its location relative to the supposed centre of origin of modern North American crayfish. The largest group of them, the Cambarinae (Cambaridae), are thought to have originated in central Mexico in the Late Cretaceous (Ortman 1905). Ancestors of modern *Procambarus* and *Cambarellus* are thought to have migrated from Mexico to the mid-southern United States (Pennak 1978). The Eryminae extended into the Cretaceous of North America and other areas (Glaessner 1969; Schram 1986). The extent and nature of the ecological interactions of these groups would be of interest.

Enoploclytia porteri sp. nov. occurred in strata that are thought to represent overbank deposits. However, a stream deposit, the Newspaper Sandstone Bed, is near by. Probably the species was a stream dweller (in the stream in which the Newspaper Sandstone Bed was deposited?) and the specimen was washed into the overbank area during a flood where it was buried almost immediately before the specimen could disassociate. Unfortunately, the comparative morphology of the fossil actually reveals little about its natural history so it is not possible to confirm the supposition that the species was a stream dweller. Modern crayfish exhibit extreme diversity in habitat and food preferences and considerable morphological variation exists among species within similar habitats (e.g. the size of the first chelae of modern stream forms varies considerably (Pennak 1978)).

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